

# First complete heterosoricine shrew: A new genus and species from the Miocene of China

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Heterosoricinae are the oldest known soricids, their records dating back to the middle Eocene of North America and earliest Oligocene of Eurasia. They became extinct during the Miocene and were thus far only known from dental and cranial remains. For the first time, a virtually complete heterosoricine is described, coming from the early/middle Miocene locality of Shanwang, Shandong Province, which is famous for the diversity and excellent preservation of its fossils. *Lusorex taishanensis* gen. et sp. nov. is closely related to *Wilsonosorex* from the early Hemingfordian of North America. Both are unusual in sharing well-developed conules on the upper molars and reduced ectocingulids on the lowers, and most likely these sister taxa reflect faunal exchange between North America and NE Asia in early Miocene time. *L. taishanensis* was the size of a European common shrew, *Sorex araneus*. The heavy masticatory apparatus of the new heterosoricine contrasts with its slender postcranial skeleton. Adaptively, *L. taishanensis* appears to be similar to the North American *Blarina brevicauda* in its strong masticatory apparatus, very short tail, and slight limb specializations toward fossorial habits. It differs from other soricids as far as is known by unfused tibia and fibula.

Key words: Soricidae, Heterosoricinae, Miocene, China, skeleton, adaptations, new taxon.

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## Introduction

Shanwang, about 22 km northeast of the county seat Linqiu in Shandong Province, China, is a former lake of early–middle Miocene age. The lake deposits are 120 m thick and consist mainly of shale and diatomite, lying on basalt and overlain by basalt (Yan et al. 1983). The site is one of a few classical Neogene localities in China and has a great reputation for the high taxonomic diversity and extraordinary preservation of its fossils, including plants and animals. Several dozens of complete and articulated skeletons of mammals have been recovered since the 1930s. Five species of small mammals and thirteen species of larger mammals have been described thus far (Young 1937, 1977; Wang 1965; Li 1974; Zhang 1974; Xie 1979; Qiu 1981; Yan et al. 1983; Qiu et al. 1985, 1986; Qiu and Sun 1988). Biochronologically, the Shanwang Local Fauna is referred to the late Shanwangian Chinese Land Mammal Age and can be correlated with the late Orleanian European Land Mammal Age and the European Land Mammal Zone MN 5 (Li et al. 1984; Qiu and Qiu 1995). This correlation is based mainly on the co-occurrence of *Hemicyon*, *Chalicotherium*, *Plesiaceratherium*, and *Lagomeryx* with rather complicated antlers, the latter first appearing in Zone MN5 (Mein 1999).

This paper describes a new heterosoricine shrew from Shanwang on the basis of a virtually complete skeleton and

dentition. It represents the only complete heterosoricine known to date and provides for the first time information about the postcranial skeleton in this subfamily. In addition to teeth, only lower jaws and rostral skull fragments are known from previously described heterosoricines.

The assignment of the new taxon to heterosoricines is based on a suite of mandibular and dental characters: The horizontal ramus of the mandible is deep and massive, the temporal fossa is not pocketed, and the well excavated masseteric fossa is subdivided by a horizontal crest. Upper and lower molars have a compact form, and P4 and M1–2 have no emargination of the distal outline and thus no posterior projection of the hypoconal flange.

## Systematic paleontology

Order Soricomorpha Gregory, 1910

Family Soricidae Fischer von Waldheim, 1817

Subfamily Heterosoricinae Viret and Zapfe, 1951

Genus *Lusorex* nov.

Figs. 1–6.

Type species: *Lusorex taishanensis* sp. nov.

Etymology: After Lu, Chinese abbreviated form of Shandong Province, the provenance of the fossil, and *sorex* (Latin) for shrew.



Fig. 1. *Lusorex taishanensis* (holotype), early–middle Miocene of Shanwang, Shandong Province, China (IVPP V 13915). The soft body “shadow” is preserved in black.

**Diagnosis.**—First and second upper and lower molars resemble those of *Wilsonosorex* Martin, 1978. Differs from *Wilsonosorex* by its undivided mesostyle (well-divided in *Wilsonosorex*), crest-like and Y-shaped metaconule (a high pointed cusp in *Wilsonosorex*), and weaker paraconule of M1–2 (strong and doubled in *Wilsonosorex*); discontinuous ectocingulid below protoconid and hypoconid (below protoconid only in *Wilsonosorex*), and very sharp, laterally compressed entoconid of m1–2 (less crest-like in *Wilsonosorex*). Small size as in *W. bateslandensis*. Additional diagnostic features include rather small first upper and lower incisors. Differs from all other heterosoricine genera in having well-developed conules on upper molars and reduced ectocingulids on lowers. Postcranial skeleton essentially soricid-like. Differs from other subfamilies, as far as known, by unfused tibia and fibula.

*Lusorex taishanensis* sp. nov.

**Holotype:** A virtually complete skeleton with preserved soft body outline. Dentition of right side completely preserved. Collection of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing, V 13915.

**Type locality and horizon:** Shanwang (Diatomite quarry), Linqu County, Shandong Province, China. Early–middle Miocene (Late Shanwangian, MN 5 equivalent).

**Etymology:** *Taishanensis*, in allusion to the Taishan Mountain, one of the five celebrated mountains of China, which is located close to the fossil site.

**Diagnosis.**—As for genus.

**Measurements**

Tooth measurements in mm (P4–M3 greatest length × greatest width, other positions greatest length only; A = antemolars between 1st incisor and 4th premolar):

**Upper teeth.**—A1 1.24; A2 0.40; A3 0.60; A4 0.28; A5 0.80; P4 1.96×1.68; M1 1.68×1.92; M2 1.44×1.68; M3 0.84×1.28.

**Lower teeth.**—i1 3.36; a1 0.88; a2 0.52; a3 0.64; a4 0.44; a5 0.88; m1 1.84; m2 1.60; m3 1.28.

Skeletal measurements in mm (greatest length); in parentheses measurements of an adult specimen of extant *Sorex araneus*:

Skull and body (premaxilla to pubis) 63.0 (62.4); skull 19.2 (19.7); tail ~24.5 (47.7); humerus 8.0 (7.4); ulna 10.5 (10.5); radius 7.5 (7.8); hand 6.9 (7.3); pelvis 11.5 (11.8); ilium 6.0 (5.5); femur 8.5 (7.8); tibia 11.3 (13.3); fibula 9.7 (fused to tibia over most of its length); hind foot 10.0 (11.8).

Indices of limb segments; in parentheses *Sorex araneus*: crural index (tibia:femur × 100) 133 (170); intermembral index (humerus + radius : femur + tibia × 100) 78 (72).

**Description**

**Dentition.**—The teeth are heavily pigmented. The dental formula is 1-6-3/1-5-3.

The first upper incisor is rather small. The medial tine is broken off yet there is not much doubt that the tooth was fissident. The broad apex is strongly curved ventrally.

There are five crowded, single-rooted upper antemolars between the first incisor and P4. The roots incline progressively toward the vertical from A1 to A5. A1 is distinctly

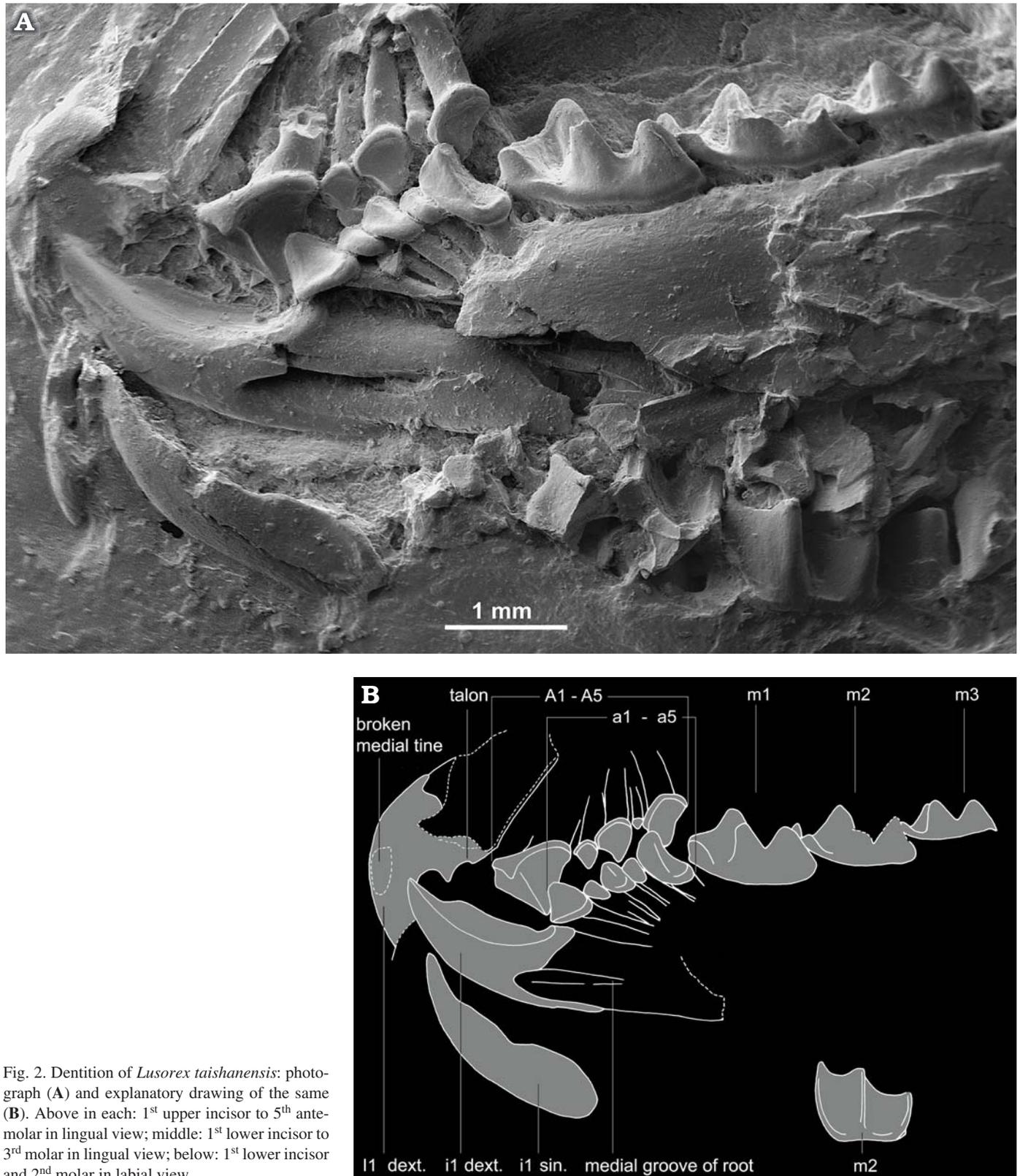


Fig. 2. Dentition of *Lusorex taishanensis*: photograph (A) and explanatory drawing of the same (B). Above in each: 1<sup>st</sup> upper incisor to 5<sup>th</sup> antemolar in lingual view; middle: 1<sup>st</sup> lower incisor to 3<sup>rd</sup> molar in lingual view; below: 1<sup>st</sup> lower incisor and 2<sup>nd</sup> molar in labial view.

larger than A2–5. It has a pointed and high anterolabial cusp. A sharp ridge runs from its apex transversely to a lingual cingular cuspule and subdivides the occlusal surface into a shallow anterior ledge and an expanded posterior basin. The laterally

compressed posterior wall of the main cusp delimits the labial tooth margin. A2, A3, and A5 exhibit an anterolabial cusp and a flat distolingual heel. A5 has a sloping distolabial ridge. The minute peg-like A4 is squeezed between A3 and A5.

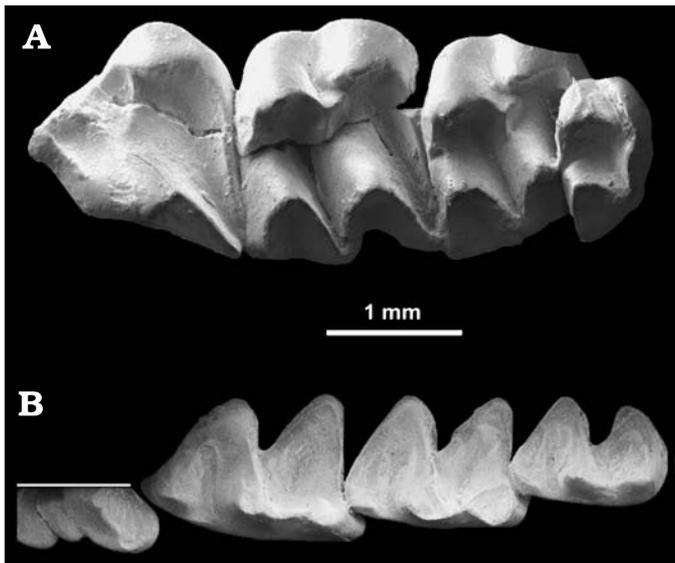


Fig. 3. *Lusorex taishanensis*. A. 4<sup>th</sup> upper premolar to 3<sup>rd</sup> molar in occlusal view. B. 3<sup>rd</sup> to 5<sup>th</sup> lower antemolar (partially) and 1<sup>st</sup> to 3<sup>rd</sup> molar in occlusal view. White line delimits antemolars that are concealed by the upper antemolars.

P4 is sub-triangular, with the labial side being much longer than the lingual one. The paracone is high and pointed, and has two weak sloping anterior crests extending to the precingulum. The posterior wing of the paracone is sharp and separated by a small notch from the postcingulum. The protocone is small and crest-like; its anterior and posterior arms are continuous with the pre- and postcingulum, respectively. The parastyle is small. The posterior basin is deep. A thin ridge connects the protocone to the base of the paracone. A hypocone is absent.

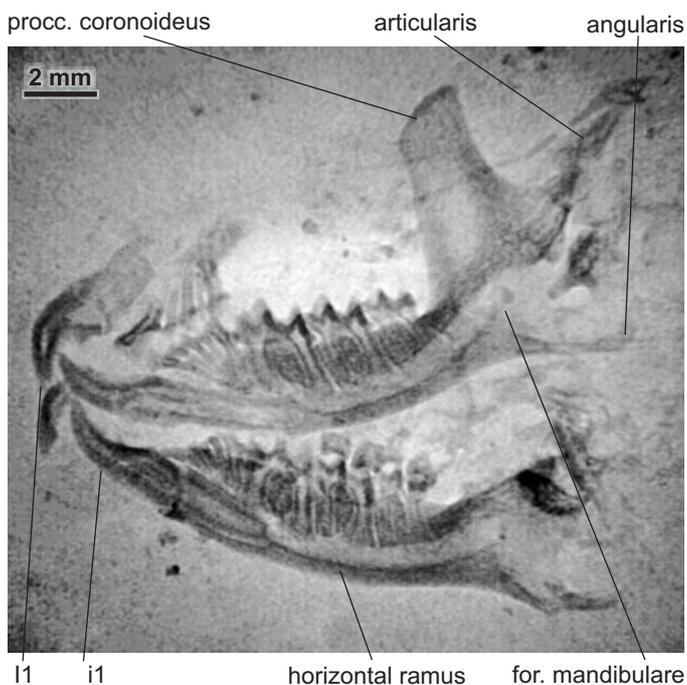


Fig. 4. X-ray image of dentition and lower jaws of *Lusorex taishanensis*.

The upper molars decrease in size from M1 to M3. M1 and M2 are sub-rectangular in outline. The width of the ectoloph is subequal to the inner half of the teeth transversely. The cusps are high and sharp; the inner cusps are anteroposteriorly compressed into a wide V-shape. Protocone, paracone, and metacone are of subequal height; the hypocone is lower. The mesostyle is undivided, para- and metastyle are ridge-like, and the preparacrista of M1 is shorter than the postmetacrista. The hypocone is isolated anteriorly from the postprotocrista by a deep valley. The paracnule is small and its anterior and posterior arms are short. The metaconule is ridge-like; the premetaconule crista terminates at the base of the metacone, and the shorter postmetaconule crista is directed posteriorly. Thus, the two metaconule wings and the postprotocrista create a crest-like Y-shaped pattern. The prominent postcingulum closes the deep transverse posterior basin. The M2 is similar to M1, except for the subequal lengths of prepara- and postmetacrista. The M3 is reduced distally. The premetacrista is continuous with the postcingulum; distinct metacone, hypocone, and conules are lacking. The postprotocrista terminates posteriorly in the trigon basin.

The first lower incisor, like the upper, is rather small for a heterosoricine shrew. Its spatulate apex is gently curved upwards, the cutting edge is smoothly bicusate, and the enamel is not wrinkled. The strong root exhibits a deep longitudinal groove along the lingual side.

The five antemolars between the first incisor and m1 are very crowded. They are inclined anteriorly and single-rooted; the roots incline progressively toward the horizontal from a5 to a1. The crowns overlap each other widely. The a1 and a5 (interpreted as p4) predominate in size, a1 being slightly larger than p4. The a1 has a high and sharp main cusp on the anterolabial corner and a broad, flat and posterolingually expanded heel. Weak lingual and posterior cingulids are visible. The a2 is small; its asymmetric chevron-shaped crown is composed of a low main cusp anteriorly and a slightly posterolingually expanded heel. The a3 resembles a1 but is distinctly smaller and lower. The very small a4 is squeezed between a3 and p4; it is morphologically similar to a2. The p4 is longer than wide and has an ovate occlusal outline. The high main cusp has a flat posterior face with a distinct posterolingual sloping ridge; its apex is antero-posteriorly compressed. The tooth shows a flat and slightly sloping heel and a weak continuous cingulid along the lingual and distal margins. The root of p4 is very strong.

The lower molars are graded in size. All cusps are very slender and piercing. The entoconid is sharp and laterally compressed. The metaconid and entoconid are of the same height and somewhat lower than the protoconid; the paraconid is lower than metaconid and entoconid, and the hypoconid is lowest. The oblique cristid terminates anteriorly beneath the protocristid notch. The postcristid joins the posterior wall of the entoconid directly, it is fused with the entoconid and there is no postentoconid valley. There is a deep V-shaped talonid notch between metaconid and entoconid.

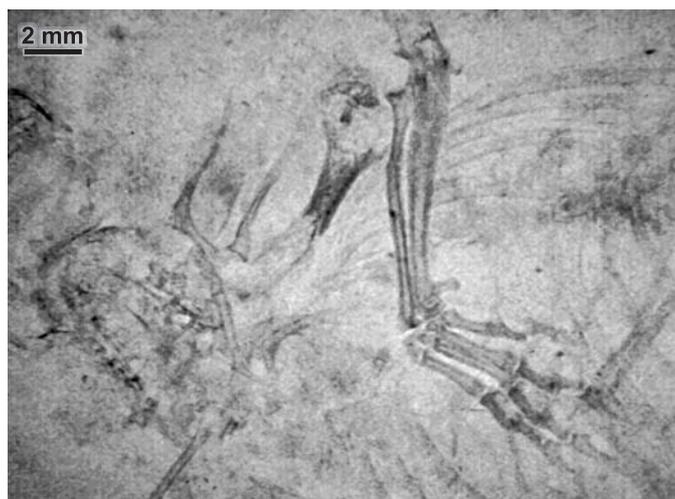


Fig. 5. X-ray image of the forelimb of *Lusorex taishanensis*.

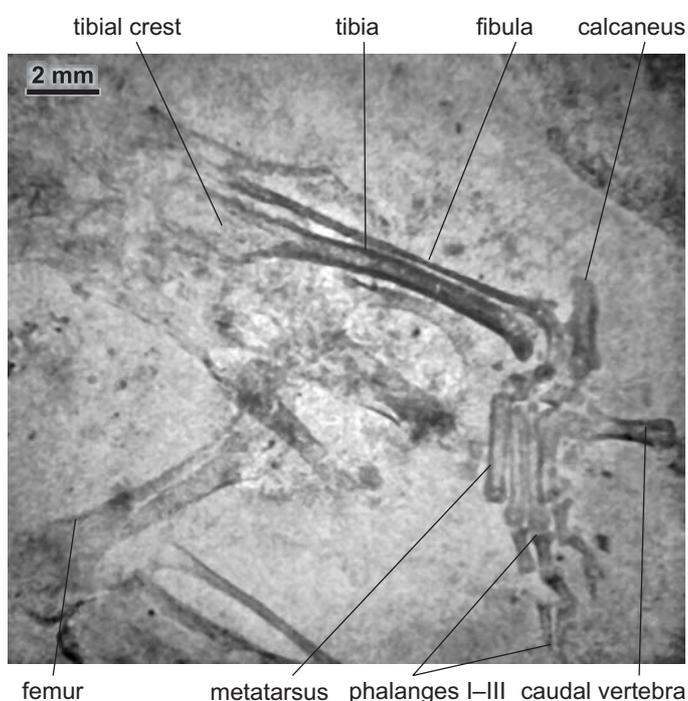


Fig. 6. X-ray image of the shank and hindfoot of *Lusorex taishanensis*.

The cingulids are weak and discontinuous at the bases of the protoconid and hypoconid. The trigonid basin is open lingually, and the deep hypoflexid opens at the level of the ectocingulid. The talonid of m1 is wider than the trigonid. The m2 closely resembles m1 except for the subequal width of trigonid and talonid. The m3 is basically similar to m2, but its talonid is narrower than the trigonid.

**Skeleton.**—No skull details are accessible. The horizontal ramus of the lower jaw is deep and robust. The coronoid process is strong and apically rather wide. X-ray photos reveal a long styliform angular process that is characteristic of shrews in general. The temporal fossa is deeply excavated but not

pocketed. The masseteric fossa is well-excavated and subdivided by a horizontal crest. The condylar process exhibits two articular facets separated by a rather long and thin interarticular bridge. The mandibular foramen is wide and located in a depression below the crest-like ventral border of the temporal fossa.

The vertebral column includes 7 cervical (most likely), 13 thoracic, 6 lumbar, probably 3 sacral, and probably 13 caudal vertebrae. The caudals are simple and slender. The clavicles are well-developed. The scapula shows a narrow outline, a high spine, and a long acromion, which is apparently bifurcated. The pelvis has a straight ilium, a wide obturator foramen, and a narrow process of the pubis, which originates from the ventro-caudal edge of the pelvis. We cannot totally dismiss the possibility that the pubic spines formed a symphysis. It seems, however, more likely that a true pubic symphysis is absent. The pubic condition may compare to that of soricomorphs such as the American shrew mole, *Neurotrichus gibbsi*, where there is no true symphysis but a small tendinous band between the pubic spines (see Reed 1951).

The humerus is gently bowed in anterior view. The well-developed teres tubercle and part of the pectoral ridge are discernible on the right humerus. Both terminate almost halfway down the bone. The extension of the distal end of the humerus compares with that of extant shrews in general. Ulna and radius are somewhat stronger than in *Blarina*. The olecranon is relatively long and slightly inclined anteriorly. The posterior crest (see Reed 1951, for definition) of the ulna is well-developed, particularly opposite the semilunar notch and the coronoid process. The presence of a proximal ridge on the olecranon cannot be substantiated since that area is damaged on both ulnae. The radius is almost straight. Only the distal carpal row is exposed on the right hand. The trapezium is largest, followed in size by the hamatum. The distal phalanges of the hands are relatively robust, their dorsopalmar thickness being greater than in *Blarina*. They are rather straight.

The femur is straight and shows a well-developed third trochanter distal to the greater trochanter. The shank departs morphologically from that of other soricids by its unfused tibia and fibula. However, the fibula is tightly pressed against the tibia along the distal half of the bones, and proximally they diverge like in other shrews. Thus, the fused and unfused condition are functionally most likely about the same. The falciform process of the tibia is well-developed and extends along the proximal third of the bone. Few details of the hind foot can be substantiated. The tuber calcanei is well-developed, and the distal phalanges appear to be rather straight.

## Comparisons

Martin (1978) described the new genus *Wilsonosorex* together with two new species from early Hemingfordian deposits on the Great Plains, USA. Both species, *W. conulatus* from the Martin Canyon beds at Quarry A, Colorado, and *W. bateslandensis* from the Flint Hill Local Fauna, South Da-

kota, were based on characters of the first and second upper molars. First and second lower molars, found at the same localities, were associated by Martin (1978) only with reservation with the uppers. The dentition of the new Chinese heterosoricine confirms this association now without doubt.

*Wilsonosorex* is an unusual heterosoricine and *Lusorex* corresponds to most of its highly diagnostic characters (but see Diagnosis for differences), including:

- distinct paraconules and metaconules on M1–2;
- protocone plus conules of M1–2 anteriorly compressed into a sharp V-pattern, with hypocone making a separate short V next to and twinned with the protocone;
- ectoloph and inner half of M1–2 of subequal length;
- cusps of upper and lower molars high and pointed;
- ectocingulid of m1 discontinuous below protoconid (in *Lusorex* also below hypoconid);
- postcristid of m1–2 confluent with the entoconid;
- small size.

We consider *Wilsonosorex* and *Lusorex* as closely related sister taxa, resulting from faunal exchanges between NE Asia and North America, most probably in early Miocene time. In Tedford et al. (1987) the North American Quarry A and Flint Hill Local Faunas are considered early Hemingfordian and around 18–19 Ma. The European Neogene Land Mammal Zone MN 5, the presumable correlate of the late Shanwangian Chinese Land Mammal Age, is later, around 15–17 Ma according to Steininger (1999). Plausible candidates for the ancestry of these unique shrews are unknown, however, from either North America or Asia. One of the most striking features of *Wilsonosorex* and *Lusorex* is the presence of distinct conules. We consider this a plesiomorphic character for heterosoricines but it is unknown from heterosoricine taxa of earlier occurrences in North America, Asia, and Europe (and from the subfamily in general). To our knowledge upper molars of the genera *Quercysorex* Engesser, 1975, Eocene/Oligocene of Europe, *Gobisorex* Sulimski, 1970, Oligocene/Miocene of eastern Asia, and *Mongolosorex* Qiu, 1996, Miocene of eastern Asia, are unknown. The respective lowers, however, do not appear to be especially similar to the m1–2 of *Wilsonosorex* and *Lusorex*, e.g., they exhibit a continuous and well-developed ectocingulid on m1 while it is weak and discontinuous in the latter genera.

Martin and Green (1984) tentatively assigned two M1 and one m1 from the Hemingfordian age Black Bear Quarry II locality in the Rosebud Formation, South Dakota, to *Wilsonosorex* sp. They suggested that the specimens possibly represent a new heterosoricine genus. The Hemingfordian *Wilsonosorex* sp. is clearly distinct from *Lusorex* in features such as the well divided mesostyle and anteroposteriorly less compressed protocone and hypocone of M1, and the continuous ectocingulid on m1.

The only other taxon that shows some detailed resemblance to *L. taishanensis* is *Pseudotrimylus roperi* (Wilson, 1960) from the early Hemingfordian of Quarry A, Colorado. We accept Gureev's original classification and confine the genus *Pseudotrimylus* to include only the type species *P.*

*roperi*. *P. roperi* is similar to *L. taishanensis* in a combination of characters such as: undivided mesostyle of M1–2, fusion of postcristid and entoconid of m1–2, well-developed entoconid of m3, occlusal morphology of A1, and division of the masseteric fossa on the lower jaw (see Engesser 1979: pl. 8c; Wilson 1960: fig. 21d; Wilson 1963: fig. 1). *P. roperi* departs widely, however, from *L. taishanensis* in features such as: Absence of conules on M1–2, distinct hypocone on P4, strong ectocingulids on m1–2, enlarged and slightly wrinkled first lower incisor, trapezoidal outline of P4, and dental formula 1-5-3/1-4-3 (see Engesser 1979: pls. 6b, 8b, c; Wilson 1960: figs. 14, 16; Wilson 1963: fig. 1).

## Discussion

*L. taishanensis* compares in size with the extant European common shrew (*Sorex araneus*) except for its distinctly shorter tail and shorter tibia and hind foot (see Measurements). The lengths of the segments of the hindlimbs of *L. taishanensis* show more isometry than in *S. araneus*. The higher crural index of *S. araneus* (see Measurements) suggests enhanced cursorial abilities, while the indices of the limb bones, the rather robust forearms and ungual phalanges of the hand, and the very short and weak tail of *L. taishanensis* appear to indicate more fossorial habits. Semiaquatic species such as the European water shrew, *Neomys fodiens*, are long-tailed and have a still higher crural index than *S. araneus*.

The very strong and heavy masticatory apparatus of *L. taishanensis* contrasts with its delicate postcranial skeleton and it is also a striking difference between *L. taishanensis* and *S. araneus*, where the lower jaws and the dentition are much more slender. Among living shrews the North American short-tailed shrew, *Blarina brevicauda*, also exhibits a short tail, relatively strong forearms and hands, and a relatively heavy dentition, and it may represent adaptively an analogue of *L. taishanensis*. *B. brevicauda* is the most fossorial of American shrews and constructs surface and subsurface runways and subterranean burrows. Its diet consists of invertebrates such as insects and snails, small vertebrates, and plant items.

The outline of the black soft body “shadow” is ovate. The tail was obviously covered with short and sparse hairs. Ear pinnae and details of body hair cannot be substantiated. More preparation of the specimen will show whether gut contents are preserved.

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